A Review of Ecological Factors Affecting the Annual Cycle in Island Populations of Seals[1]

JOHN K. LING[2]

ABSTRACT: Colonization of island habitats by pinnipeds for all or part of their life cycle may expose the populations to various pressures. While the advantages of an island rookery must override the disadvantages for such a situation to be selected, its most efficient utilization by one or more species can be achieved only by coordination of the annual cycles within and between species. Certain age categories or species must make way for others at critical phases of the annual cycle if habitat preferences are the same. However, more than one age group or species can coexist when habitat requirements do not overlap. Interspecific strife is reduced to a minimum by either spatial, temporal, or behavioral separation, but deleterious interspecific contact may occur. Intraspecific strife between different age classes is prevented by variable annual cycles with respect to age, but within any narrow age category such interaction as occurs may affect the number of females being fertilized and thereby act as a regulator of population size.

SEALS TEND TO INHABIT the more remote regions in the higher latitudes of the globe and many species are found only on islands in some of the world's stormiest seas. Orr (1965) believes that unfavorable contact with large terrestrial predators over a long period of time, including harassment by man more recently, has led to an avoidance of easily accessible zones by pinnipeds. Scheffer (1958) has remarked on the fairly rapid evolution of certain genera of island-dwelling seals, and it is reasonable to suppose that behavioral and ecological speciation have proceeded along with morphological differentiation and changes in population size. Within the narrow framework of its annual cycle a species ought to survive, but disturbance of the seasonal pattern may have damaging consequences. The ways of life in insular colonies are so well adjusted to the prevailing conditions that it can only be concluded that the life cycles of the species concerned have evolved slowly under the pressures of natural selection. Occupation of islands by seal colonies must therefore have been going on for a considerable time.

The contingencies of an island way of life cannot be neatly categorized because of their interacting nature. These factors include the physical environment and inter- and intraspecific competition for space and food. The significance of this competition varies inversely with the size of the island or, more correctly, the amount of suitable space and available food. An annual time table which is geared to the species' best advantage with respect to these limitations will be selected for by an evolving population.

The foregoing remarks could apply equally well to animals anywhere, not just pinnipeds confined to lonely islands. But islands have proved their worth in the past for demonstrating important biological principles; and in the present context of a restricted and restrictive environment many features in the timing of the annual cycle can be emphasized. The purpose of this paper is to examine briefly the interrelationships between various phases in the annual cycle of some of the world's better known seal populations occupying numerous small oceanic islands, in order to provide such emphasis.

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[2] Department of Botany and Zoology, Massey University, Palmerston North, New Zealand. Present address: Department of Biology, University of Newfoundland, St. John's, Newfoundland, Canada.

WORLD DISTRIBUTION OF ISLAND SEAL POPULATIONS

The world's seal populations and their distribution have been thoroughly treated by Scheffer (1958). Their geographic range extends through 70 degrees or more in latitude north and south of the equator. Island colonies are often important not only in terms of size but also for their well documented biology. Many pinniped populations throughout the world were decimated almost to the point of extinction by sealers during the early nineteenth century. Latterly, rigid protection, followed by enlightened management policies with regard to some commercially exploitable stocks, has resulted in a steady increase and ultimate stabilization of numbers in many colonies. However, the effects of near extermination and recolonization in the face of human interference may be recognized today by changed population structures and the possible presence of species different from the original occupants (Csordas, 1962). In the absence of reliable data concerning former island pinniped populations the real nature of such changes, if any, probably will never be resolved.

In the southern hemisphere the great subantarctic island colonies of elephant seals (*Mirounga leonina*) now rank among the most exhaustively studied and best known wild mammal populations. The largest herds are at South Georgia (Laws, 1953, 1956*a*, 1956*b*, 1960), Macquarie Island and Heard Island (Carrick and Ingham, 1960, 1962*a*, 1962*b*, 1962*c*; Carrick, Csordas, and Ingham, 1962; Carrick, Csordas, Ingham, and Keith, 1962), and Kerguelen Island (Angot, 1954; Paulian, 1953). A number of species of fur seals also occupy many islands in middle southern latitudes and are the subject of increasingly intensive study. These include the South African (Cape) fur seal (*Arctocephalus pusillus*) (Rand, 1954, 1956), Kerguelen (South Georgia) fur seal (*A. tropicalis gazella*) (Paulian, 1964; Bonner, 1968), New Zealand fur seal (*A. forsteri*) (Csordas and Ingham, 1965), and the Tasmanian fur seal (*A. tasmanicus*) (Warneke, 1966).

Small islands along the California and Mexican Pacific coasts contain the now rapidly increasing stocks of northern elephant seal (*Mirounga angustirostris*) which are providing classical data on population growth and structure (Bartholomew, 1952; Bartholomew and Hubbs, 1952, 1960; Radford et al., 1965). Large aggregations of California sea lion (*Zalophus californianus*) and Steller sea lion (*Eumetopias jubata*), and smaller numbers of harbor seal (*Phoca vitulina*) and northern fur seal (*Callorhinus ursinus*) also occur on these islands, and interesting aspects of species interaction and population turnover are provided by them (Bartholomew and Boolootian, 1960; Orr, 1965; Orr and Poulter, 1965; Rice et al., 1965; Peterson and Bartholomew, 1967). Major concentrations of the northern fur seal occur on the Pribilof Islands, Alaska, and to a lesser extent on the Robben and Commander Islands in the North Pacific Ocean. Roppel and Davey (1965) trace the history of this, the most intensively studied pinniped species. Also extant from the Aleutian Islands to British Columbia are the majority of the world's population of Steller sea lions (Kenyon and Rice, 1961). A northern Pacific tropical island species is the Hawaiian monk seal (*Monachus schauinslandi*), the general biology of which is well documented (Kenyon and Rice, 1959; Rice, 1960; Wirtz, 1968). Another tropical island species is the Galapagos sea lion (*Zalophus californianus wollebaeki*) of which there are several hundred animals (Orr, 1967).

There are several small but significant colonies of grey seals (*Halichoerus grypus*) on offshore islands around Great Britain. These are also yielding important data on breeding biology and population dynamics exemplifying further the factors involved in an island existence (Hewer and Backhouse, 1960; Hewer, 1964; Boyd, 1963; Coulson and Hickling, 1964). Grey seal colonies also occur on islands off the east Canadian coast, and these provide extremely interesting comparisons with their eastern Atlantic counterparts (Mansfield, 1966).

FACTORS IN THE ISLAND LIFE OF SEALS

General Considerations

The most significant features of an island life involve the sharing of available space and food resources for which competition will occur both between and within species. Because of the

aquatic feeding habits of seals, data are available only in respect to competition on land.

The vagaries of the external environment are probably of no greater or less significance to island populations than to mainland forms. If anything, there are certain advantages in sheer physical isolation for an island species, especially since the problems of making a landfall on a tiny land mass, often after long migrations, appear to have been solved by most pinnipeds. Shelter from the elements assumes minor importance in the island environment once the problem of getting there has been overcome, but suitable habitat must be available for the purposes of the island stopover.

Interspecific Competition

There are many examples of interspecific relationships between pinnipeds cited in the literature. Scheffer (1958) noted the coexistence of up to six species of pinnipeds in favorable areas, but interspecific contact has not always resulted in mutual toleration of two or more species, and there are instances of one species apparently being affected adversely by another.

Orr and his colleagues, working on small islands off the California and Mexican Pacific coasts, have provided some graphic examples of interspecific behavior among pinnipeds (Orr, 1965; Orr and Poulter, 1965; Rice et al., 1965). Brief reappraisal of these authors' results indicates the extent to which interspecific reactions may be involved in the annual cycle of island populations of seals (Table 1). Competition for space during breeding activity could pose problems if annual cycles of the most numerous species coincided and habitat preferences were the same. It is evident from Table 1 that the situation on Año Nuevo Island is a very well-ordered one with breeding activities occurring at such time and place as to involve little or no interspecific disturbance. This suggests a certain plasticity in response to environmental stimuli controlling seasonal activities in the various species. There is often close, nonaggressive contact between male California sea lions and nursing female Steller sea lions when the numbers of the former are increasing quite rapidly and numbers of the latter are still high (Orr, 1965). Moreover, habitat preferences preclude any major deleterious intrusion by California sea lions upon Steller cows. Although present-day

TABLE 1
HABITAT PREFERENCES AND SEASONAL MAXIMUM AND MINIMUM NUMBERS OF PINNIPEDS ON AÑO NUEVO ISLAND, CALIFORNIA: 1961–1964
(Based on data in Orr and Poulter, 1965)

SPECIES	PREFERRED HABITAT	SEASONAL MAXIMUM	SEASONAL MINIMUM	OTHER REMARKS
Steller sea lion (*Eumetopias jubata*)	Large outlying rocks	July–August (2,500)	March–May (400)	Move northward after breeding in June–July
California sea lion (*Zalophus californianus*)	Sandy beaches near water's edge; inner reefs or rocks	September (13,000)	February–March (500)	
			June–July (0)	Breed in southern and Baja California during June–July
Northern elephant seal (*Mirounga angustirostris*)	Sandy beaches in higher and drier parts	April–May (450)	July–August (25)	Breeding season: January–February
Harbour seal (*Phoca vitulina*)	Shoreline and bays; rocks uncovered at low tide	July (100)		Small numbers; only slight fluctuations
Northern fur seal (*Callorhinus ursinus*)	Outlying rocks			Occasional stragglers, but primarily pelagic away from breeding islands in Bering Sea

numbers of elephant seals are relatively small, the population may have been higher in early times, when some competition for space could have occurred with California sea lions. However, the annual cycles are governed so that these two species attain maximum numbers at different times of the year and such competition does not arise.

Northern elephant seals and California sea lions coexist quite amicably on islands off Baja California. As a rule, the two species form separate aggregations, but close interspecific contacts are often made, while only one deliberate attack by an elephant seal on a sea lion has been witnessed. Harbor seals are much more timid and avoid contact with elephant seals and California sea lions (Bartholomew, 1952; Peterson and Bartholomew, 1967).

Between 1930 and 1960 the numbers of California sea lions occupying the California Channel Islands increased from about 1,900 to more than 13,300, while Steller sea lion numbers fell from approximately 2,000 to 50 in the same period. Changes in seawater temperatures with concomitant shifts in distribution of food species may account for the replacement of Steller sea lions by California sea lions. Alternatively, the latter may have ousted the former by pressure of numbers on the same haul-out areas (Bartholomew and Boolootian, 1960). Nonbreeding California sea lions may be near the northern limit of their geographic range on Año Nuevo Island, where Steller sea lions breed successfully (Orr and Poulter, 1965). Steller sea lions and northern fur seals breed together on the Pribilof Islands (Scheffer, 1958).

A small colony of northern fur seals was reported to be breeding on San Miguel Island, California, which is also inhabited by numerous California sea lions and northern elephant seals (Peterson, Le Boeuf, and Delong, 1968). Several instances of interactions between fur seals and sea lions were cited, but photographs of the area suggest that space is not limited.

At Macquarie Island, Antarctica, fur seals were extremely abundant when the island was discovered in 1810, but within a decade they were virtually exterminated without even the identification of the species being reliably established. There is now a small but apparently increasing colony of about 500 New Zealand fur seals (Csordas and Ingham, 1965). Southern elephant seals were also reduced almost to

FIG. 1. New Zealand fur seals (*Arctocephalus forsteri*) on typical rocky habitat, Macquarie Island.

extinction, but the population is now believed to have stabilized at its original abundance of approximately 110,000 individuals (Carrick and Ingham, 1962*c*). The two species presently occupy quite different habitats and are rarely seen together. The fur seals lie out on rocky headlands (Fig. 1) from which they slip quickly into the sea when disturbed, while elephant seals favor the sandy beaches (Fig. 2) and tussock grass hinterland during their breeding and moult haul-outs. It seems unlikely that any overlap of habitat by the two species would have occurred even before the fur seal population suffered serious reduction at the hands of the sealers, although this cannot be substantiated in the absence of precise knowledge as to former numbers or species of fur seal.

Breeding of the southern elephant seal takes place in September and October, 80 percent of pups being born in the three-week period around October 17 (Carrick, Csordas, Ingham, and Keith, 1962). The fur seal breeds during December and January (Csordas and Ingham, 1965), and this period coincides with the moult haul-out of immature elephant seals of both sexes and mature females, which favor sandy beaches and deep, muddy wallows, respectively. Fur seal numbers are maximal at the end of February when large subadult male elephant seals frequent the beaches and tussock areas to undergo their annual moult, but absolute numbers are not as high as during the breeding season. Both the annual cycles and habitat preferences of the two principal pinniped species which were possibly the original mammalian inhabitants of Macquarie Island are therefore adjusted so that any conflict between them will be minimal.

The only direct interspecific contact I have observed during two summer trips to Macquarie Island (in 1962–1963 and 1963–1964) involved the New Zealand sea lion (*Phocarctos hookeri*) and elephant seals. Occasionally male sea lions haul out in the course of their oceanic wanderings (Gwynn, 1953; Csordas, 1963) and there is often a dispute between a sea lion and elephant seals over a resting place on the beach (Fig. 3). This is resolved either by one or the other disputant retreating or, quite frequently, the sea lion settling down among the elephant seals. Gwynn (1953) described the

FIG. 2. Moulting subadult male southern elephant seals (*Mirounga leonina*) on typical beach habitat, Macquarie Island.

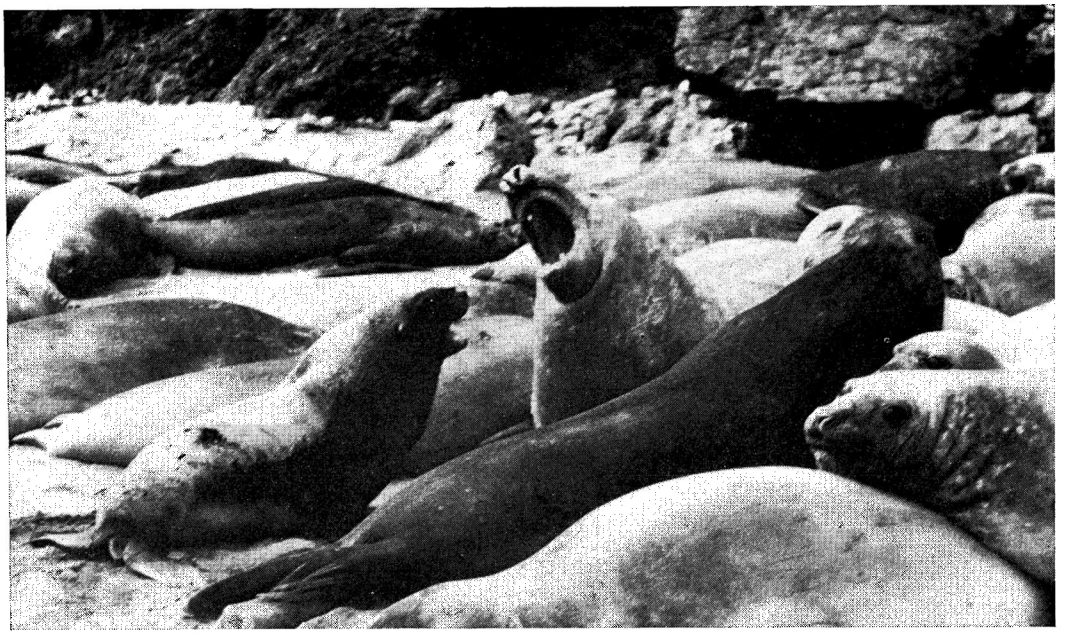

FIG. 3. Interaction between New Zealand sea lion (*Phocarctos hookeri*) and adult male southern elephant seals (*Mirounga leonina*), Macquarie Island.

activities of sea lions during the elephant seal breeding season when a certain amount of disturbance ensued both in harems and among weaned pups. Nursing elephant seal cows were quick to ward off intruders, but the weaned pups were sometimes attacked. *Phocarctos hookeri* frequents the beaches and tussock, but on Macquarie Island there are never more than a few stragglers. In fact, this species breeds on New Zealand subantarctic islands further north which are infrequently visited by elephant seals, so that deleterious contact between the two species does not take place. However, a change in the habits of either or both species could bring them into more direct competition with one another.

At Macquarie Island I have also seen sea lions lying out on rocky platforms surrounded, at some distance, by fur seals. No clashes between the two species were witnessed, but it would appear that the fur seals are afraid of the sea lions, since they always keep their distance.

Temporal overlap of breeding seasons of southern elephant seals and fur seals (*Arctocephalus tropicalis gazella*) occurs to some extent at South Georgia. However, breeding elephant seals do not come into contact with breeding fur seals, but wandering juvenile elephant seals and moulting adults often stray into fur seal breeding territories. Here the harem bulls threaten the elephant seals, but actual contact or biting is rare. Thus some disturbance of fur seal breeding activities may be said to occur as a result of these interspecific reactions which may be expected to intensify as the fur seal numbers increase (Bonner, 1968). Only a major change in timing of the annual cycle of these species would remove them altogether from contact with one another. Bonner does not speculate on the situations which may have existed when fur seal numbers were much greater, in the days before commercial sealing operations decimated the populations.

Intraspecific Competition

Crowding of a seal population on a small island may result in severe intraspecific competition if the annual cycle is not adjusted with respect to age and sex. Even the absence of a substantial part of the total population may not entirely alleviate the effects of too many animals utilizing an inadequate resource, be it space or food.

A portion of the immature third of the total

Macquarie Island elephant seal herd hauls out during the winter months, but this component leaves the rookery just before the commencement of the breeding season, thereby making way for reproductively active bulls and cows and, later on, the latters' pups, which occupy the beaches during the spring and early summer. Ease of access to the beach by gravid cows hauling out to pup seems to determine the location of harems rather than availability of preferred habitat, and the breeding population is not spread evenly over the rookery (Carrick, Csordas, and Ingham, 1962). The behavior of bulls is restricted to maintenance of the harem as a functioning entity and not towards retention of territory. Space is apparently not a limiting factor in reproductive success.

Pups-of-the-year and immature seals together constitute about two-thirds of the total population just after the breeding season has ended. The pups remain on the island for some 5 to 6 weeks after being weaned at about 3 weeks, and immature seals of both sexes return later to moult. A large proportion of these age groups lie out on the beaches not long since vacated by the last of the breeding adults.

A certain amount of intraspecific squabbling occurs throughout the year as seals of either or both sexes are often packed closely together during their seasonal haul-outs. However, these interactions do not reflect any active striving for suitable space which at no time of the year is fully utilized. The point to be made is that phases of the annual cycle can be closely synchronized with respect to the different age categories, since the island habitat can accommodate all animals of this species which come ashore at any one time. The island is an ideal assembly point for elephant seals during the breeding season, and their inherent gregariousness may increase reproductive efficiency.

It has been suggested that intraspecific competition for adjacent food resources by elephant seals at Macquarie Island acts as a homeostatic self-regulator of population size (Carrick, Csordas, Ingham, and Keith, 1962). Such competition is believed to be generated between older and younger sexually mature seals of both sexes. Thus older and presumably more experienced and demanding gravid females would compete for food with sexually mature virgin cows as these two categories converge on the island precincts before hauling out to pup and then mate again, or simply to mate. Similarly, more aggressive old bulls might compete with younger subadults for the same food resources. The result of this intraspecific strife at Macquarie Island is said to be retarded sexual maturity compared with that of the same species at South Georgia where, until recently, a commercial cropping program operated which kept numbers below the level at which competition would intervene.

Chapman (1961) proposed a direct role of food in limiting the size of northern fur seal populations on the Pribilof Islands, where further increase in numbers is believed to be restrained through pup mortality due to malnutrition. This in turn is said to arise from the need for nursing mothers to travel long distances in search of food at the expense of their milk supply and to the detriment of the suckling pup. (Mortality on land is also attributed to hookworm parasites.) While arguments for or against the merits of these theories are beyond the scope of this paper (see McLaren, 1967 for discussion), it is instructive to consider the implications of such mechanisms with respect to the annual cycles of the species concerned, since changes in the timing of events are involved in at least one instance.

Attainment of sexual maturity in the southern elephant seal is marked by a change in the annual time table to the extent that the moult takes place later, and the autumn-winter haul-out of about a quarter of the immature population is abolished almost entirely (Carrick, Csordas, Ingham, and Keith, 1962). Of the cows, only those which pup during the previous breeding season moult later. Primiparous cows do not switch to the later moulting pattern until after the birth of their pups the following year; and barren cows are also believed to moult along with the immature seals (Gibbney, 1957). Moulting is also retarded in adult bulls which are ashore for the breeding season. The delay is proportional to the degree of reproductive activity which in turn governs the length of the fast and subsequent recuperation at sea (Carrick, Csordas, Ingham, and Keith, 1962). Ling (1965*a*) suggested a hormonal inhibition of hair growth in breeding elephant seals, but it seems just as likely that a direct nutritional block may operate alone or in conjunction with

the fast undergone during the breeding season haul-out. Carrick, Csordas, Ingham, and Keith (1962) have already suggested nutrition as a factor in delayed maturity.

The nutritional stress imposed on the northern fur seals of the Pribilof Islands may also be expected to cause a delay in reaching sexual maturity as compared with another population for which long-distance foraging is not a necessity. However, there are no data to resolve this question.

Coulson and Hickling (1964) suggested density-dependent calf mortality arising from crowded breeding conditions as a mechanism for controlling growth of the grey seal population on the Farne Islands, Northumberland. If calf mortality is the factor limiting growth of the grey seal populations, it seems unnecessary to postulate the additional regulating mechanism of delayed sexual maturity. There are insufficient data available on the age of sexual maturity in the various grey seal colonies around the British Isles to determine if in fact such retardation occurs, especially since Hewer (1964) pooled his data to derive several population parameters for this species.

Hawaiian monk seals appear to breed biennially, although they are capable of reproducing annually and there is no biological reason for them not doing so (Rice, 1960). The carrying capacities of the islands inhabited by this species are not fully utilized, so that a nutritional curtailment of reproduction cannot be invoked. Rice predicts that eventually a density-dependent food-limiting factor will be involved in arresting and stabilizing the growth of the monk seal population. The reproductive rate of about 16 percent is low compared with the figures of 60 to 80 percent reported for other species. Nevertheless, the birth rate had improved since an earlier study (Kenyon and Rice, 1959), and the population may be slow in reaching its potential rate of increase following severe decimation of the stocks during the middle of the nineteenth century. The great preponderance of adults (68 percent) over subadults, yearlings, and pups (18 percent) is indicative of a stagnant population and quite the reverse of the situations seen in other species. Moreover, Wirtz (1968) reported a high incidence of missed pregnancies among Hawaiian monk seals compared with other phocids. The pup mortality has not yet been accurately established for this species.

Thus, although mortality rates in the first year of life of the grey seal, northern fur seal, and southern elephant seal are of the same order of magnitude (40 to 60 percent), in the latter there are grounds for believing that a delayed switch to the adult annual cycle may also operate in stabilizing the size of the herd.

Habitat

Island habitats may be very prone to changes through physical or biotic agents. Natural weathering and erosion are physical changes which are inevitable but slow. Biotic factors can include a species' own activities as they affect its habitat; an example is the formation of wallows and flattening of other rest areas by elephant seals, thereby hastening erosion of what often is a quite unstable substrate. Introduced species such as the sheep (*Ovis aries*), European rabbit (*Oryctolagus cuniculus*), and the Stewart Island weka (*Gallirallus australis scotti*) at Macquarie Island have so affected the island's flora as to cause serious erosion problems (Taylor, 1955; Costin and Moore, 1960). The weka may be responsible for significant changes in the coastal tussock grass (*Poa foliosa*), a favored habitat of the southern elephant seal. Such changes, if sufficiently widespread, could affect the seasonal behavior of part of the elephant seal herd: new areas might have to be colonized, else the numbers of this species could be much reduced.

Internal Environment

Seals are well endowed with the necessary mechanical protection and thermal insulation demanded by any conditions encountered during oceanic migrations or island haul-outs (Sokolov, 1960; Ling, 1965*a*). A seasonal requirement and one important facet of the annual cycle is the maintenance and renewal of an outer covering to withstand the effects of long immersion on the one hand and a prolonged stay ashore on the other. Also associated with a seasonal haul-out may be the need to accumulate a supplementary energy source in the form of subcutaneous depot fat. Neither of these features is peculiar to an island-frequenting animal, but

seasonal changes in the integument must be geared to the annual cycle imposed on an island form on the one hand or a mainland form on the other.

Timing of the annual cycle may be controlled by day length which will of course vary with latitude. As a general rule, equatorial cycles tend to be more protracted and indefinite than those of higher latitudes. For example, the breeding season of the Galapagos sea lion (*Zalophus californianus wollebaeki*) extends over a 6-month period from September to February compared with only 2 months (June to July) in the same species in California and Mexico (Orr, 1967; Peterson and Bartholomew, 1967). Breeding and moulting are also more protracted in the Hawaiian monk seal than in species occurring nearer the poles (see Fig. 4). This may be due not so much to photoperiodic (or other) influences as to the lack of any biological need for a precise time table in less rigorous latitudes. Adjustment of the annual cycle to environment becomes really critical for island populations nearer the polar regions in order that they may capitalize on optimal seasonal conditions which are usually of only short duration. When several species are involved concurrently at the same or different places, a very delicate coordination is required for the proximate stimuli to evoke the desired ultimate response.

SELECTED EXAMPLES OF ANNUAL CYCLES

Further discussion is best pursued using actual examples of annual cycles in a few

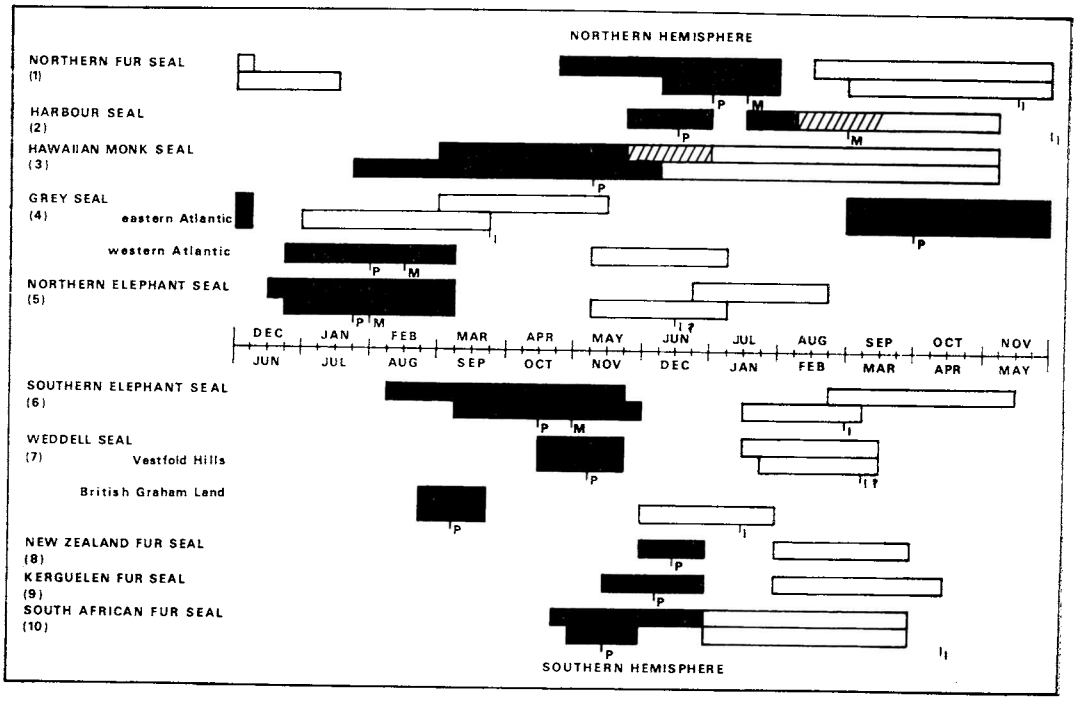

FIG. 4. Annual cycles of selected pinnipeds. Northern hemisphere and southern hemisphere seasons have been made to coincide by adjusting the calendars to a 6-month phase difference. Male cycles are plotted above female cycles, except where only female cycles are shown. Key: *black rectangles*, breeding; *white*, moult; *cross-hatching*, concurrent breeding and moult; *M*, mating date; *I*, implantation date; *P*, parturition date (approximate peaks). Numbers refer to sources of data as follows: (*1*), Scheffer, 1962; Scheffer and Johnson, 1963; Craig, 1964. (*2*), Harrison, 1963. (*3*), Kenyon and Rice, 1959. (*4*), Backhouse and Hewer, 1956, 1957; Boyd, 1962; Mansfield, 1966. (*5*), Bartholomew, 1952; Orr and Poulter, 1965. (*6*), Laws, 1956*a*, 1956*b*; Gibbney, 1957; Carrick, Csordas, Ingham, and Keith, 1962; Ling, 1965*a*. (*7*), Wilson, 1907; Bertram, 1940; Lugg, 1966. (*8*), Csordas, 1958; Csordas and Ingham, 1965. (*9*), Ling, 1965*b*; Paulian, 1964; Bonner, 1968. (*10*), Rand, 1954, 1956.

selected species of seals. These are shown diagrammatically in Figure 4. Whereas the harbor seal varies its annual cycle according to clines along the northeastern Pacific seaboard (Bigg, 1968), the annual cycles of many island species are very precisely timed and synchronized over a wide breeding range. Around the British Isles, the grey seal breeds from mid-October to late December at the Farne Islands (Coulson and Hickling, 1964) and in September and October from Pembrokeshire to the Hebrides, with some evidence of spring (March) breeding also (Boyd, Lockie, and Hewer, 1962; Hewer, 1957; Hewer and Backhouse, 1960; Backhouse and Hewer, 1957). In the western Atlantic the grey seal breeds on islands and pack ice in January and February, and in the Baltic it breeds in March and April, again on ice. It is interesting too that on ice and uncrowded islands the species is monogamous, whereas around the British Isles and on crowded ice-free islands east of Nova Scotia there appears to be either incipient polygamy or promiscuity (Fisher: in Harrison, 1963; Mansfield, 1966). This and the white birth-coat suggest that the grey seal may have been originally a pagophilic species breeding monogamously in midwinter in time for the pups to be weaned, fasting for a time, and then dispersing in spring in the zooplankton-rich waters of the North Atlantic Ocean. In the more temperate parts of its range, autumn breeding is now the rule. The ecological significance of this contrast continues to puzzle students of pinniped behavior.

The life histories of elephant seals and grey seals parallel each other quite closely, but the actual timing of the events in the annual cycles does not always coincide. The annual cycle of the grey seal around the British Isles is seasonally out of phase, by exactly half a year, with both northern and southern elephant seals. However, the annual cycles of the western Atlantic grey seal and the northern elephant seal run according to similar time tables which must be regarded as the more primitive patterns. Breeding behavior in virgin elephant seal cows is not well understood spatially or temporally, but mating is believed to take place in the water during the normal breeding season (Laws, 1956*a*). Similarly, virgin grey seals mate in more remote areas and may even pup in late winter or spring around the British Isles (Harrison, 1963). In view of these observations one might ask whether behavior and the annual cycle of immature and maturing seals reflect the endogenous and/or ancestral pattern.

Elephant seals and grey seals fast for periods of days, weeks, or even months during their seasonal haul-outs, and this undoubtedly imposes a considerable physiological strain on the animals. Phocids in general, and *Mirounga* in particular, are highly adapted to an aquatic life (Laws, 1959); yet the latter's reproductive phases are perhaps more closely tied to land than is the case in any other pinniped. Because it is so ill-adapted to a terrestrial habitat, the elephant seal has evolved an annual cycle in which the land phases are restricted and as brief as possible in breeding females. The annual cycles of *Mirounga* and *Halichoerus*, therefore, have rather clearly defined phases: breeding, feeding, and moulting; and the interrelationship of these phases involves a controlling mechanism to an acute degree. The ultimate factor in the annual cycle of the southern elephant seal is the need to ensure that young-of-the-year are weaned onto a favorable food supply. The pivotal point in the cycle, then, is the pupping date which is determined by the gestation period and the time of blastocyst implantation. A relationship has been sought between the end of moult and implantation (Laws, 1956*b*; Carrick, Csordas, Ingham, and Keith, 1962). The moult date in females varies with sexual condition, but the date of implantation must be no less accurately synchronized than the date of pupping. The free blastocyst period enables this well-synchronized breeding season, with its high concentration of seals, to be followed by a recuperative phase before gestation resumes and thereby sets the time table for the next cycle. The fact that attendance at the breeding season imposes a later moult date on seals of both sexes strongly suggests that hair-shedding—preceded by subcutaneous follicular activity of some 6 to 8 weeks' duration (Ling and Thomas, 1967)—is delayed either by the presence of hair growth inhibiting gonadotrophins or adrenocorticotrophin, or by the influence of a direct nutritional block consequent upon the reproductive fast.

The northern fur seal, which also assembles in vast breeding concentrations on North Pacific islands, has a well synchronized breeding season too. Ovulation occurs a few days after parturition, but lactation is prolonged and the nursing mothers feed during the suckling period. However, harem bulls fast during the breeding season. Since otariids are well adapted to their terrestrial habitat, the breeding haul-out may be less demanding relative to that of the elephant seal—though Bonner (1968) reported several cases of suspected stress, resulting sometimes in death, among harem bulls during the breeding season at South Georgia, and death through fighting is common among northern fur seals (Johnson, 1968). The moult in both sexes of the northern fur seal follows shortly after breeding and is more prolonged, and the animals feed and blastocyst implantation occurs during the process. There is a progressive delay in the timing of the moult with respect to age, but the annual retardation is greater in females than in males. Thus, by the tenth year of age the mid-date of the male moult is 32 days earlier than the mid-date of the female moult (Scheffer and Johnson, 1963). A sharply defined switch from one regime to another upon the attainment of sexual maturity does not take place. Reproductive hormones circulating at the time of ovulation may well inhibit the initiation of hair growth, but nutritional status appears to be such as to allow a new pelage cycle to commence shortly afterwards.

Annual cycles of the New Zealand, Kerguelen, and South African fur seals are all very similar both in duration and season, although the two subantarctic species are later by about one month. In the absence of detailed information on the duration of their moults, it appears that implantation may occur after the pelage change has terminated. This contrasts with the northern fur seal which implants during the moult.

The time table of the northern elephant seal closely resembles that of its southern counterpart but is not quite 6 months out of phase—seasonally it breeds some 2 months earlier, commensurate perhaps with its lower northerly latitude. Judging from the available data, the durations of the various phases are the same for both species. The annual cycle of the more tropical Hawaiian monk seal is not so clearly defined, and the different phases are more protracted and may even merge with one another.

A population spread over an extensive mainland range may show a gradation in seasonal timing of the annual cycle. Whereas the southern elephant seal over its circumpolar, subantarctic range displays a remarkably well synchronized annual cycle—undoubtedly selected for equally well synchronized circumpolar optimal conditions—the annual cycle of the Pacific harbor seal is clearly graded into a clinal pattern, again offering selective advantage. The Antarctic mainland Weddell seal (*Leptonychotes weddelli*) also shows considerable spatial variation in its annual time table, the constancy of which from place to place and year to year has not been accurately assessed. Five subspecies of the harbor seal (*Phoca vitulina*) and three of the South American fur seal (*Arctocephalus australis*) are recognized, and there may be two of the Phillip fur seal (*A. phillipi*) (Scheffer, 1958): all are distributed in a north-south direction along mainland coasts of the Americas. It is interesting to speculate if the annual cycles of all three species show clinal variation and whether such incipient speciation is also manifest in the Weddell seal. The annual cycles of at least two populations of the latter on opposite sides of Antarctica differ in timing by about 8 weeks (Bertram, 1940; Lugg, 1966). Also significant, perhaps, is the fact that a continental species such as the harbor seal learns to swim very soon after birth, because of the quieter inshore waters and ready availability of resting areas for the youngsters. Moreover, harbor seals and Weddell seals do not migrate over long distances but remain more or less closely attached to the land mass or ice throughout the year. Separate populations with their own annual time tables could become established in such sedentary forms.

SUMMARY AND CONCLUSIONS

Colonization of an island by large aggregations of pinnipeds of one or more species during phases of their annual cycle offers many singular advantages of biological importance: reproductive efficiency, mutual protection, and population regulation. Potential disadvantages or prob-

lems may be included under the general heading of inter- and intraspecific competition for food and space with all the attendant implications. The same kinds of factors operate between and within species to ensure that the presence of one component is not deleterious to another and so, through natural selection, the annual cycles have become adjusted with respect to species, age, and sex.

There is a strong tendency on the part of seals to return to their birthplace year after year for breeding, and synchronization of the annual cycle is important to ensure reproductive success. It would seem that there is selective advantage in breeding on small islands, crowded conditions notwithstanding. The stringencies of an island existence demand a biological thriftiness, however, else selection will operate through infant mortality or delayed maturity in limiting the population. Migratory forms may utilize more than one locality, including an island or islands, during the year. Their coming and going allows a more efficient exploitation of the advantages offered by an island rookery. Different habitat requirements will also permit more than one species to occupy an area offering a choice. Thus we have temporal and spatial economy which may be manifest in multispecific use of what might otherwise be a rather restricted resource. The annual cycle is a very plastic feature of an island-dwelling species which allows for an ebb and flow in response to population pressures.

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